

Abstract—The timing and duration of the reproductive cycle of Atka mackerel (*Pleurogrammus monopterygius*) was validated by using observations from time-lapse video and data from archival tags, and the start, peak, and end of spawning and hatching were determined from an incubation model with aged egg samples and empirical incubation times ranging from 44 days at a water temperature of 9.85°C to 100 days at 3.89°C. From June to July, males ceased diel vertical movements, aggregated in nesting colonies, and established territories. Spawning began in late July, ended in mid-October, and peaked in early September. The male egg-brooding period that followed continued from late November to mid-January and duration was highly dependent on embryonic development as affected by ambient water temperature. Males exhibited brooding behavior for protracted periods at water depths from 23 to 117 m where average daily water temperatures ranged from 4.0° to 6.2°C. Knowledge about the timing of the reproductive cycle provides a framework for conserving Atka mackerel populations and investigating the physical and biological processes influencing recruitment.

Timing and duration of mating and brooding periods of Atka mackerel (*Pleurogrammus monopterygius*) in the North Pacific Ocean

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Atka mackerel (*Pleurogrammus monopterygius*) is distributed along the edges of the North Pacific Ocean and adjoining basins in rocky shelf regions near landmasses and archipelagos, and in rocky reefs atop prominent bathymetric features rising from the sea floor (Rutenberg, 1962; Allen and Smith, 1988). Atka mackerel is one of the most abundant groundfish in the central and western North Pacific Ocean (Zenger, 2004) where it is a key prey item for marine fishes, birds, and mammals (Murie, 1959; Kenyon, 1965; Sinclair and Zeppelin, 2002). Modern large-scale commercial trawling by U.S. and foreign fishing vessels began during the latter half of the twentieth century, and since the end of the joint venture fishing in 1989, total landings of U.S. fishing vessels have averaged 54,000 metric tons annually (Lowe et al., 2006).

Knowledge about the timing of the reproductive cycle and temporal use of nesting habitat is essential for understanding processes affecting the recruitment and population dynamics of Atka mackerel, and for making management decisions regarding

commercial fishing activity. Despite Atka mackerel's relatively high abundance and value to the ecosystem, surprisingly little is known about its life history and ecology. Access to Atka mackerel is difficult and costly because the species inhabits a vast and remote region that is notorious for inclement weather and rough seas. Studies on the reproductive biology of Atka mackerel are further limited by a general lack of knowledge about the location of spawning and nesting sites in these remote areas. In the eastern North Pacific Ocean off the coast of Kamchatka Peninsula, there are only a handful of known spawning and nesting sites (Zolotov, 1993), and in the central and eastern North Pacific Ocean, the geographic and bathymetric distribution of spawning and nesting sites was completely unknown until recently (Lauth et al., in press).

Previously published studies have used ovarian condition to determine the start and end of the spawning period (Gorbunova, 1962; Zolotov, 1993; McDermott and Lowe, 1997), but very little has been done to investigate the time spent by males in

Manuscript submitted 23 February 2007 to the Scientific Editor's Office.

Manuscript approved for publication 24 July 2007 by the Scientific Editor.

Fish. Bull. 105:560–570 (2007).

either establishing nesting territories before spawning or in brooding eggs afterwards. Only from the western North Pacific Ocean is there published information on the nesting period from beginning to end, but methods and results have been vague and have relied on catch data from various nonstandardized fishing gears and methods (Gorbunova, 1962; Zolotov, 1993). Egg incubation times are useful for approximating the end of the male nest brooding period (Gorbunova, 1962; Lauth and Blood, 2007), however, controlled rearing experiments at a wider range of water temperatures are needed to accurately determine how the rate of embryonic development is affected (Lauth and Blood, 2007).

The objective of this study was to clarify Atka mackerel's temporal use of breeding habitat by investigating the timing and duration of nesting, spawning, and brooding phases in the North Pacific Ocean. This study makes use of *in situ* visual and behavioral observations of male Atka mackerel and an incubation model that synthesizes data from laboratory incubation experiments, egg mass collections from three different nesting sites, and descriptions of embryonic development from a companion manuscript (Lauth and Blood, 2007).

Materials and methods

Direct observation of nesting behavior

Visual and behavioral observations from time-lapse video and data from archival tags were used for determining the beginning and end of the nesting period (i.e., the duration of male territoriality), and to document nesting behaviors before the onset of spawning. Sexual dichromatism (Medveditsyna, 1962; Rutenberg, 1962) and behavioral changes in males (Nichol and Somerton, 2002; Lauth et al., in press) are primary indications of nesting activity. Nest guarding males are distinguished by their bright yellow or orange color and dark black vertical stripes. When males are breeding, they defend a nesting territory for long periods and refrain from vertical migrations. Sexually mature females or non-spawning Atka mackerel of both sexes are bluish-green or gray and typically undergo diel vertical migrations year round (Nichol and Somerton, 2002).

Time-lapse camera Diving operations to deploy and retrieve underwater camera equipment were conducted from the National Atmospheric and Oceanic Administration (NOAA) National Marine Fisheries Service (NMFS) charter vessels FV *Morning Star* (May 2002), FV *Sea Storm* (July 2002), and the United States Fish and Wildlife Service RV *Tiglax* (August 2002). A Sony Hi8 (Sony Electronics, Inc., San Diego, CA) video camera was placed inside a Plexiglas housing and secured to a mooring on the seafloor at 23 m by a diver at a known nesting site at Seguam Island, Alaska (52 22.10°N, 172 20.26°W) on 31 May 2002. The video camera had a time-lapse controller that could be set by the user to record video images at periodic intervals. The camera was attached

to a tripod frame made of welded steel. On the initial deployment, the time-lapse controller was set to record 1 minute of video each day. It was recovered on 28 July 2002 (60 days later) and reset at the same location to record 1 minute of video every hour until 7 August 2002 (a 10-day period). The camera was recovered and reset a final time to record 15 sec/h until 31 August 2002 (a 24-day period) when the camera was recovered.

Archival tags Archival tag data from a previously published study on Atka mackerel diel behavior (Nichol and Somerton, 2002) were used to infer nest-guarding behavior and to corroborate nesting periods. In July 2000, 117 Atka mackerel were captured by trawl, tagged, and released in Seguam Pass with archival tags that recorded the time, depth, and temperature once each minute (Nichol and Somerton, 2002). Commercial trawlers recovered 14 Atka mackerel with tags. Data from four of the tags were from males that showed no vertical movement for extended periods, which is consistent with nesting. Data from two of the four tags were also reported in Nichol and Somerton (2002).

Laboratory incubation experiments

Results from laboratory rearing experiments were used to develop parameters for an incubation model to determine how Atka mackerel incubation time varies between nesting sites. Laboratory experiments were conducted at the Alaska Sealife Center (ASLC) with egg masses spawned by captive Atka mackerel. In October 2002, a commercial fishing vessel with a bottom trawl collected 20 live Atka mackerel from Seguam and Tanaga Passes. The fish were kept live in tanks on board the fishing vessel and transported to the ASLC. After acclimation, antibiotic treatment, and a one-month quarantine at the ASLC, 14 Atka mackerel were transferred to ASLC exhibit tanks equipped with a submersible video camera for documenting spawning and nesting behavior. Each time an egg mass was discovered, the videotape was reviewed to determine the time of egg mass deposition. Fertilized egg masses were transferred to one of four closed-system incubation tanks consisting of a 150-L tank, recirculation pump, and a 1/3 hp inline chiller controlled by an electronic thermostat. The configuration of the system provided stable temperatures with very little fluctuation. Temperatures for the incubation chambers were chosen on the basis of *in situ* observations at nesting sites in the Aleutian Islands (Lauth et al., in press). Ten incubation experiments were conducted at four different water temperatures: three each at 4°, 5°, and 7°C, and two at 10°C. The light cycle in the aquaria was regulated with an electronic timer set at 12 h light and 12 h dark.

For all incubation experiments, hatching day for an egg mass was defined as the first day larvae hatched from the egg mass. A scatter plot of incubation temperature versus total days to first hatching was constructed for all incubation temperature trial data, and regression analysis (Zar, 1999) was used to determine how total days to hatching varied as a function of temperature.

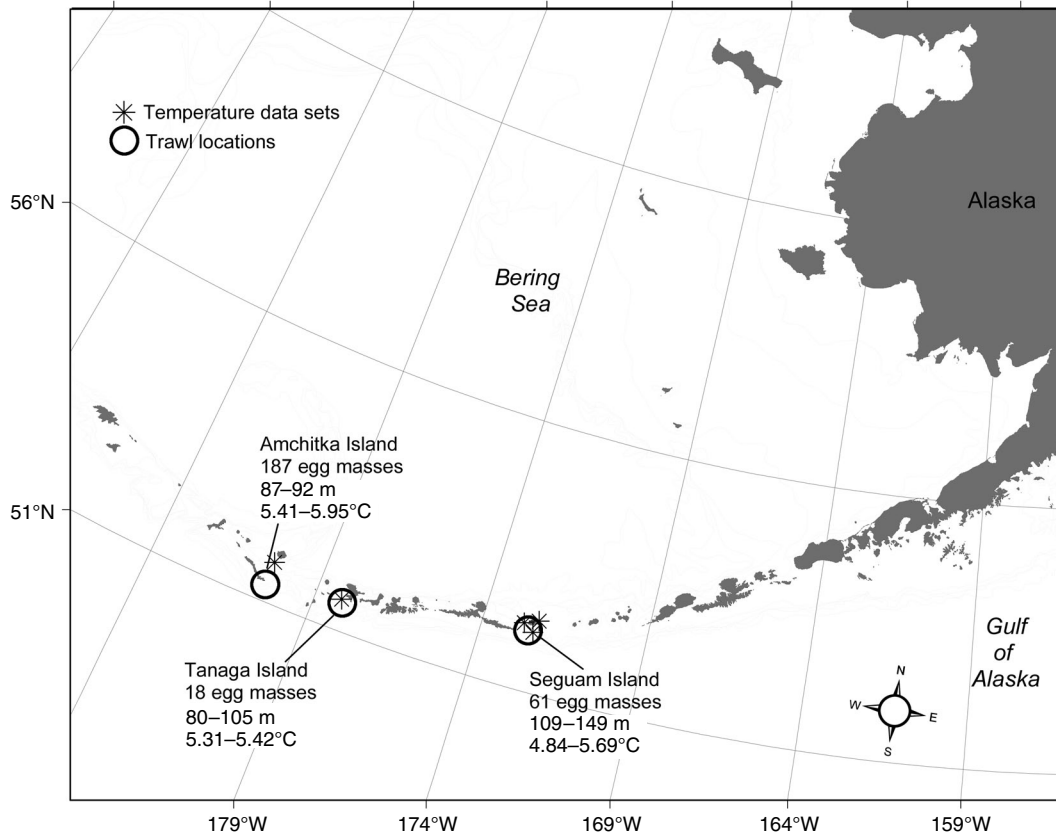


Figure 1

Map showing collection sites for water temperature data sets (asterisks; also see Table 1) and trawl locations where Atka mackerel (*Pleurogrammus monopterygius*) egg masses were collected (open circles). The number of egg masses collected and the range of water depth and temperature are listed beneath each trawling location.

Incubation model

An incubation model was used for extrapolating spawning and hatching dates for egg mass samples collected from three different Atka mackerel nesting sites. During the period 7–23 October 2004, egg masses were collected from trawl hauls aboard the commercial stern-trawler FV *Seafisher* and samples were preserved in 10% phosphate-buffered formalin. The October collection period was chosen because histological studies have indicated it is the month when spawning ends in Alaska (McDermott and Lowe, 1997). A total of 266 egg masses were collected: 187 from the Amchitka Island area, 18 from near Tanaga Island, and 61 from the waters surrounding Seguam Island (Fig. 1). In the laboratory, egg mass samples were placed underneath a stereo dissecting microscope and aged to the nearest day by using the descriptions of embryonic development from the incubation experiment described by Lauth and Blood (2007).

The calculation of spawning and hatching dates was based on the assumption that the effect of temperature on incubation rate for any given development stage was

nearly a constant linear relationship for the entire incubation period. The constant relationship is generally true for temperatures normally encountered by eggs in their habitat (Ahlstrom, 1943; Riley, 1974; Hempel, 1979). Spawning and hatching dates were estimated by using the following relationship:

$$d_t = \frac{D_t s_{6^\circ C}}{S_{6^\circ C}}$$

where d_t = age of the egg mass (days) at temperature t ;
 D_t = total incubation time (days) at temperature t ;
 $s_{6^\circ C}$ = estimated age of the collected egg mass (days) using the descriptions of embryonic development from Lauth and Blood (2007);
 $S_{6^\circ C}$ = total number of days for first egg to first hatching;

Spawning date = Egg mass collection date - d_t , and
 Hatching date = (Egg mass collection date - d_t) + D_t .

Table 1

Source, latitude, longitude, depth, and time periods for water temperature data sets from sites surrounding Amchitka/Tanaga and Seguam Islands (also see Fig. 1). PMEL EPIC = Pacific Marine Environmental Laboratory Eastern Pacific Investigation of Climate Processes.

Source	Latitude (N)	Longitude (W)	Depth (m)	Time period
Amchitka and Tanaga sslands				
PMEL EPIC buoy data	51°46.12'	179°30.70'	39	08 June 1987 to 18 June 1988
PMEL EPIC buoy data	51°35.40'	178°12.60'	142	03 May 2002 to 11 May 2003
Seguam Island				
PMEL EPIC buoy data	52°08.08'	172°25.57'	109	03 May 2002 to 01 Oct 2002
PMEL EPIC buoy data	52°08.08'	172°25.57'	109	01 Oct 2002 to 03 Nov 2002
PMEL EPIC buoy data	52°16.00'	172°45.10'	147	02 May 2002 to 10 May 2003
PMEL EPIC buoy data	52°16.00'	172°45.10'	147	19 May 2001 to 13 Oct 2001
PMEL EPIC buoy data	52°16.00'	172°45.10'	139	13 Oct 2001 to 13 Feb 2001
Atka mackerel archival tag	Exact location unknown		92	23 July 2000 to 21 Jan 2001
Nearshore current meter ¹	52°22.09'	172°20.26'	22	01 June 2002 to 01 Sept 2002

¹ The current meter was anchored to substrate within an Atka mackerel nesting site.

Values for the total incubation time of a collected egg mass (D_t) were calculated with a best-fit regression equation derived from the laboratory incubation experiments.

Temperature data sets used for determining a low and high range of D_t were obtained from buoys operated by the Eastern Pacific Investigation of Climate Processes (EPIC) program of the NOAA Pacific Marine Environmental Laboratory (PMEL; Table 1; Fig. 1). There were two EPIC temperature data sets available for the Amchitka and Tanaga Island area and five for the Seguam Island area (Table 1). The depths for the EPIC buoy data ranged from 39 to 147 m, which are close to the depth limits where Atka mackerel nesting sites were observed (Lauth et al., in press). In addition to the EPIC data sets for the Seguam Island area, two more temperature data sets were available from a shallow (22 m) and deep (92 m) Atka mackerel nesting site (Table 1). The temperature data from the shallow nesting site were collected from the data logger attached to the time-lapse camera and the data from the deep nesting site were collected from an archival tag on a male that exhibited nesting behavior. Daily water temperatures were pooled by area for calculating an average daily water temperature and standard deviation. The minimum and maximum average daily water temperatures from each area for the period 1 July to 15 January were used in the incubation model for the low and high D_t .

Egg mass spawning and hatching dates were pooled by week and ogives of the pooled data were made for a low and high range of D_t for each egg collection area. To estimate the timing of spawning and nesting periods across the entire geographical region, pooled data for both low and high temperatures from all three areas were proportioned equally, combined, and plotted by relative frequency over time.

Results

Direct observation of nesting behavior

Time-lapse camera The time-lapse camera was used for documenting the arrival of male Atka mackerel at a nesting site near Seguam Island in 2002 (Fig. 1). Divers at the site observed no males or Atka mackerel egg masses when the camera was deployed on 31 May, nor were males observed in the camera footage for the first five days. On 5 June, a bright yellow male with black vertical stripes (male nesting coloration) swam across the screen during a 10-second period. There was a similar observation on 6 June. Neither of these males exhibited territorial behavior toward a specific patch of rocky substrate. On 9 June, two males hovered close to the bottom at mid-screen in the background for the entire minute, and on 10 June, one male pursued another Atka mackerel of unknown sex, followed it (off screen), and then returned to mid-screen and hovered for the remainder of the minute. Atka mackerel were not observed with the time-lapse camera for the next two days. On 13 June, a group of three males swam across the screen in the distance. On 14, 15, and 17 June, males were observed hovering in the distance or swimming across the screen. On 18 June, a bright yellow male with dark black vertical bands was positioned in front of the camera. The same male was observed in the same area in front of the camera every day after that through 31 August (74 days). Between 18 June and 31 August, other males were periodically observed in the background exhibiting nesting behavior. During all three recoveries of the time-lapse camera, divers observed two egg masses within a 1 m radius of the camera mooring.

Archival tags Two archival tags were retrieved from Seguam Pass in September 2000, and one each in September 2001 and January 2001. It was evident from the depth data of two tags that Atka mackerel males made

regular diel vertical movements during the nonbreeding season from mid-December through May (Fig. 2, A and B). During the breeding season from June to December, the behavior of all four tagged males was characterized by an extended period of time on the bottom and very limited or no vertical movement (Fig. 2). It was assumed that these periods corresponded with nesting behavior. The earliest date within a year that such nesting behavior was observed was 4 June (Fig. 2A) and the latest was 12 December (Fig. 2B). The male in Fig. 2A was at liberty for 406 days and exhibited 89 days of limited vertical movement before being captured. The male in Fig. 2B displayed nesting behavior for 141 consecutive days,—the longest uninterrupted time period for all tagged males. Also unique to the male in Figure 2B was a depth shift from 125 to 92 m on 14 September followed by a continuation of nesting behavior until 14 December (89 days). Three of the four males displayed nesting behavior shortly after being released (Fig. 2, B–D), but two of these males (Fig. 2, C and D) abandoned the behavior after only 33 days, whereas the other male (Fig. 2B) shifted depth and continued nesting behavior. Males in Figures 2B and 2D also showed unexplained and periodic ascents and descents during periods of presumed nesting behavior.

The average depths where male nesting behavior was displayed ranged from 92 to 117 m and the water temperatures at those locations ranged from 4.5° to 4.9°C. Water temperatures varied by a maximum of 2.6°C during these periods.

Laboratory incubation experiments

In 2004, ten egg masses were fertilized and all were incubated successfully at the ASLC. The first spawning event for the captive Atka mackerel was recorded on 27 July, and the last was on 13 October. For 2005, the first and last spawning dates were 13 July and 12 October. The average temperature for each of the four treatments was 3.89°, 5.04°, 7.03°, and 9.85°C. The incubation time of 74 days at 6.15°C from Lauth and Blood (2007) was also used in the analysis. The best fit of the data was a logarithmic function with a negative slope (Fig. 3). Total incubation time (D_t) was a function of the natural logarithm of incubation temperature (t) with days to first hatching ranging from 44 days at 9.85°C to 100 days at 3.89°C (Fig. 3).

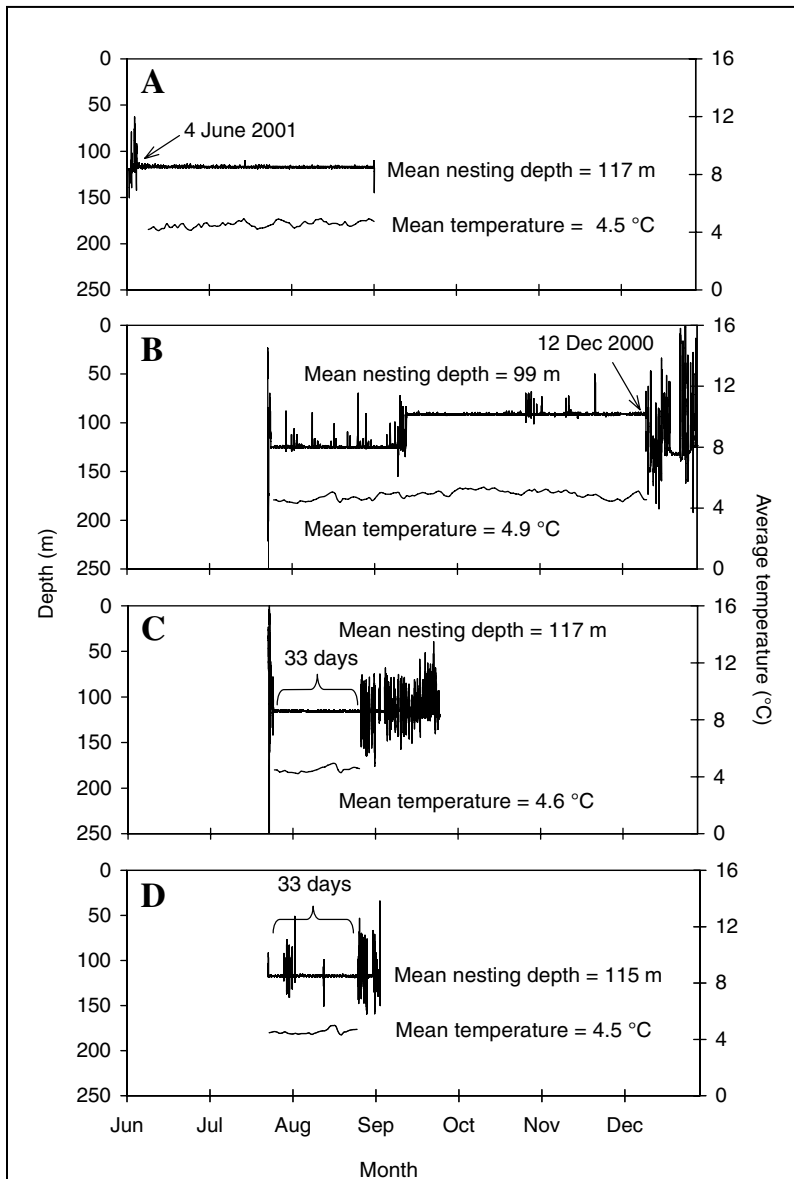
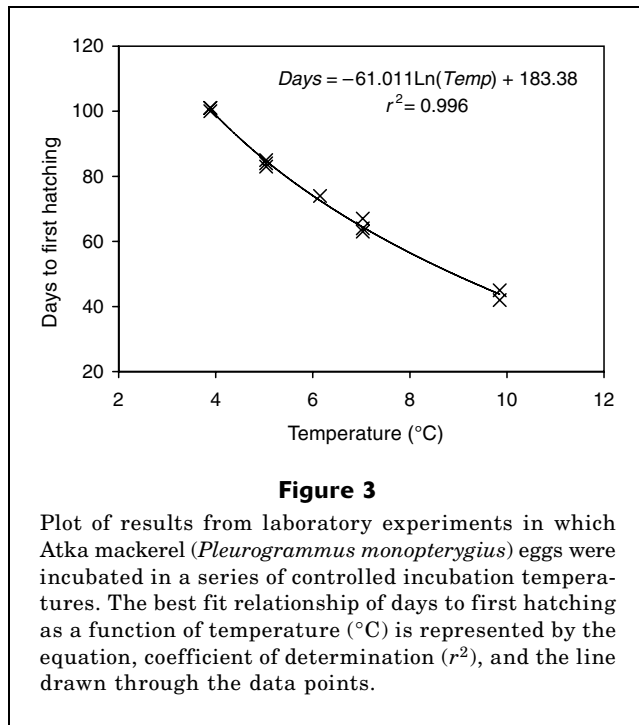


Figure 2

Plots A–D show the depth and temperature data of archival tags from four captured male Atka mackerel (*Pleurogrammus monoptygius*) that were originally tagged and released in July 2000. The calendar year for plot A is 2001, and for plots B–D is 2000. All four males exhibited periods of limited vertical movement consistent with nesting behavior. An arrow points to the start of nesting behavior in plot A and the end of nesting behavior in plot B, and plots C and D have brackets delineating the nesting periods and the length of nesting behavior (days) is indicated above the brackets. Mean water depth and temperature of nesting behavior periods are also presented along with average daily water temperature represented by the lower black line in each plot. Periods with frequent and repeated diel vertical migrations outside the arrows and brackets are consistent with non-nesting behavior.

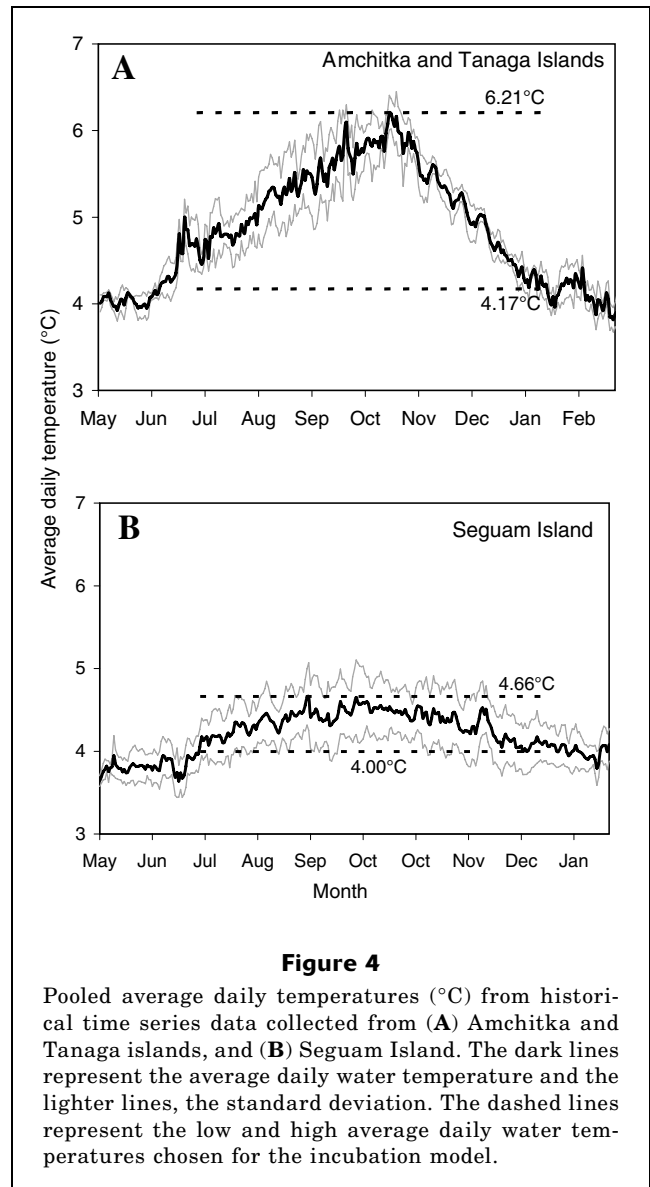


Incubation model

Water temperatures varied by area and time of year; daily averages were generally highest during the spawning and hatching periods from late summer to early winter, and higher near Amchitka and Tanaga Islands compared to Seguam Island (Fig. 4). During the period 1 July to 15 January, average daily water temperatures from Amchitka and Tanaga Islands reached a maximum of 6.21°C during October and a minimum of 4.17°C in January (Fig. 4A). Average daily water temperatures were generally lower and more variable for the same period at Seguam Island, ranging from 4.00°C in June and January to 4.66°C in August (Fig. 4B). The mean and standard deviation for all daily average water temperatures for the period 1 July to 15 January was $5.22 \pm 0.16^\circ\text{C}$ for Amchitka Island and $4.34 \pm 0.50^\circ\text{C}$ for Seguam Island.

Amchitka Island Spawning started from late-July to early August, peaked from mid-August to early September, and ended in late September (Fig. 5). Some of the egg masses collected at Amchitka Island were at an advanced stage of development; therefore hatching began about the same time that egg masses were collected in mid-October and was completed by early to mid-December.

Tanaga Island Assuming the same incubation temperatures as Amchitka Island, calculated spawning and hatching dates for Tanaga Island were about a half-month later than Amchitka Island (Fig. 5). Spawning



commenced from early to mid-August and ended in late September or early October. Hatching began in early November and ended by late December or early January.

Seguam Island Spawning and hatching dates for Seguam Island were the latest among the three areas sampled (Fig. 5). Spawning began in mid-August, peaked in mid-September, and ended in early-October. Hatching commenced in mid-November and ended from early to mid-January.

All areas and temperatures combined For all areas combined, spawning began in mid-July, peaked in early September, and ended mid-October (Fig. 6). Hatching immediately followed the end of spawning, peaked in early December, and continued until late January.

Discussion

The mating and brooding cycle (i.e., reproductive cycle) of Atka mackerel lasts from June to January. The mating phase begins with males aggregating in nesting colonies where they establish individual nesting territories. Time-lapse camera footage and archival tag data show that male Atka mackerel begin aggregating and establishing nesting territories in early June, 1.5 months before spawning commences. The reason for the lengthy nest-establishment period is unknown, but fishes that provide male parental care of eggs typically put considerable effort into choosing and preparing an

optimal nesting territory because it can be an important determinant for maximizing reproductive success (e.g., Sargent, 1982; Sikkil, 1988; Bisazza et al., 1989; Östlund-Nilsson, 2000).

The second phase of mating consists of courtship and spawning, during which time a territorial male can mate with multiple females. Spawning begins mid-July and ends in mid-October. A July to October spawning period has been corroborated by a histological study of 978 Atka mackerel ovaries from collections made across the entire North American geographical range (McDermott and Lowe, 1997), and from observations of captive spawning Atka mackerel used in the incubation experiments from the present study. Because such a high proportion of egg masses were found in later stages of development at Amchitka,

it is possible that some hatching occurred before the egg mass collections. This would have the effect of shifting the onset of the spawning and hatching period at Amchitka to an earlier time. Because egg masses collected from Tanaga and Seguam Islands were much younger at the time they were collected, it is not likely that some earlier hatching took place, especially given the low water temperatures characteristic of each nesting site.

Detailed analysis of spawning times by area, with the use of aged egg masses, indicated a later onset of and peak in spawning as spawning activity moved from west to east. Female Atka mackerel spawn an average of 4.6 separate batches of eggs during the 12-week spawning period (McDermott et al., 2007), but uncertainty about precise ambient temperatures precludes conclusions regarding the periodicity of separate spawning events and whether these events were continuous or episodic.

During the brooding phase, spawning has ended and males guard the incubating egg masses within their territory until all the eggs hatch. The duration of the male brooding phase is highly dependent on water temperature. The average water temperature of 106 nesting sites covering a broad temporal, bathymetric, and geographic range in the Aleutian archipelago was 5.4°C (Lauth et al., in press). If this water temperature represented a true mean for the entire range of Atka mackerel, the average male brooding period would be 11.5 weeks. Using a video drop camera on 30 November 2005, the principal author verified that males were still aggregated and exhibiting nesting behavior at a nesting site near Dutch Harbor, AK. Considering that egg masses are spawned until late October and that *in situ* water temperatures as low as 3.99°C are observed at nesting sites, it is plausible

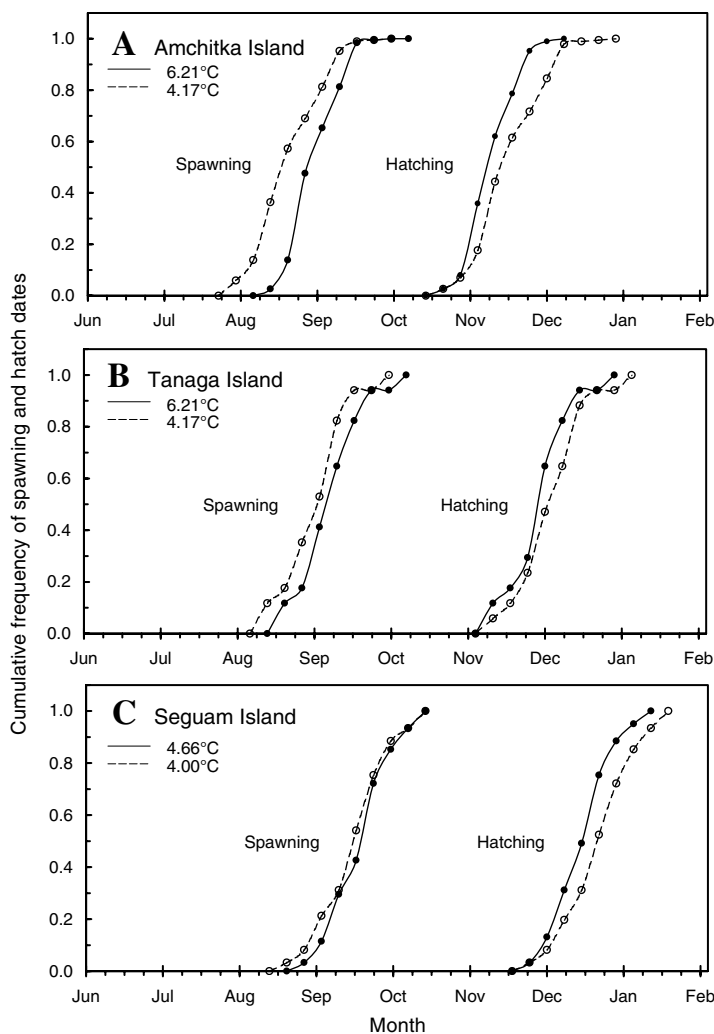


Figure 5

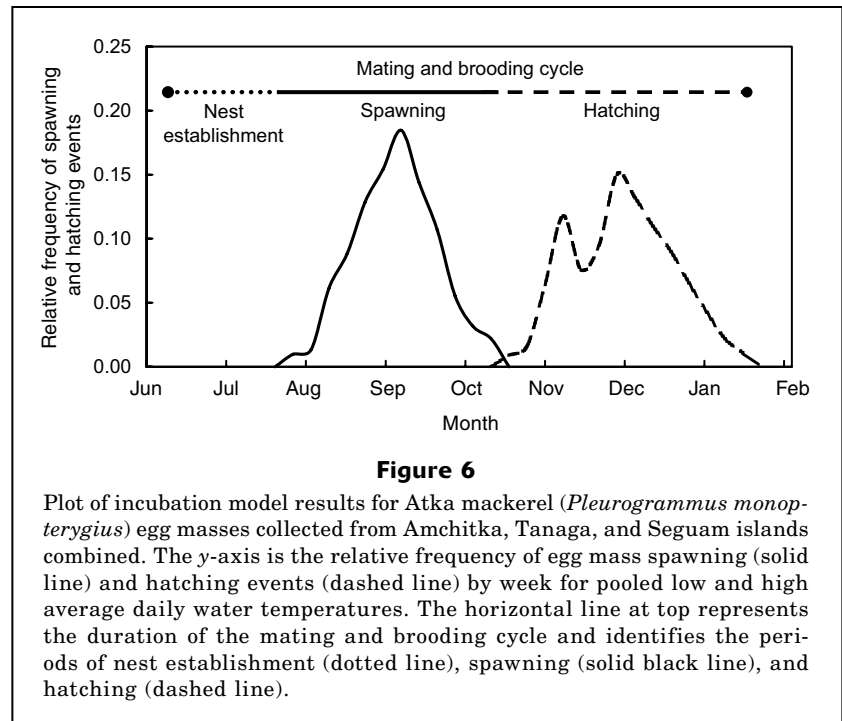
Ogive plots of incubation model results for Atka mackerel (*Pleurogrammus monopterygius*) egg masses collected from (A) Amchitka Island, (B) Tanaga Island, and (C) Seguam Island. The y-axis is the cumulative frequency of egg mass spawning and hatching dates by week for low (dashed line) and high (solid line) average daily water temperatures for each area (see Fig. 4).

that some males brood eggs at nesting sites until January.

There may be several reasons for the 2-month difference in the duration of the reproductive cycle between Alaska (7+ months) and the western Pacific Ocean (5+ months; Gorbunova, 1962; Zolotov, 1993). First, all the western Pacific Ocean nesting sites were located in coastal areas in water depths <32 m where water temperatures were likely higher and the length of the brooding period shorter than those in Alaskan waters. Second, no distinction was made between the onset of the nesting and spawning periods; that is, Gorbunova (1962) and Zolotov (1993) assumed both periods commenced in June. In Alaska, males aggregate and prepare nesting territories 1–2 months before spawning. Without a direct means for observing males at a nesting site with such tools as archival tags and time-lapse cameras, it is difficult to determine when males first arrive. Assuming a 1-month nest establishment period during May and longer incubation times for the western Pacific Ocean population, the duration of the reproductive cycle for Atka mackerel is similar to the duration of the cycle for other parts of the North Pacific Ocean.

The timing of the Atka mackerel reproductive cycle is unusual because fishes in temperate and subarctic waters typically synchronize the hatching time of larvae with periods of high zooplankton abundance in the spring or early summer (Cushing, 1990; Haldorson et al., 1993). The possible adaptive significance of hatching during the late fall and early winter may be predator avoidance, dispersal, or availability of specific prey. Atka mackerel larvae are neustonic after hatching (Kendall and Dunn, 1985) and have large mouths (Gorbunova, 1962) capable of feeding on larger planktonic prey.

The temporal, geographic, and bathymetric distribution of sampling for this study was relatively limited given the temporally and spatially complex marine environment that Atka mackerel inhabit (Ladd et al., 2005; Ohshima et al., 2005). Large-scale climate changes to the ecosystem (Rodionov et al., 2005) can cause alterations in recruitment dynamics that may affect population structure (Bailey, 2000; Ciannelli et al., 2005) and ultimately change the timing of the reproductive cycle (Hutchings and Myers, 1994; Wieland et al., 2000; Ojaveer and Kalejs, 2005). We did not investigate how water temperature or other environmental factors vary over larger scales, or how such variability influences the timing of the Atka mackerel's reproductive cycle. This study does, however, provide a framework for process-oriented investigations of stock dynamics, recruitment, and distribution of Atka mackerel populations. Time of



hatching, geographic location, and hydrographic features can all affect the dispersal of larvae and play a significant role, along with biological processes, in determining recruitment success and population structure (Napp et al., 2000).

For unknown reasons, nest fidelity varied among the tagged male Atka mackerel. Given a late July onset of spawning and relatively low ambient water temperatures at nesting sites, it is unlikely that males are able to successfully tend, from start to end, more than one brood of egg masses per season. Nests are commonly composed of eggs from multiple females (Lauth et al., in press) deposited over the 3-month spawning period and by the time the first batch of eggs hatches, the spawning period is nearing completion or has ended.

It appears that none of the four archival tags contained data from a nesting male for the duration of one complete mating and brooding cycle. All four males were captured, tagged, and released while the breeding season was underway in late July. The first male (Fig. 2A) did not exhibit nesting behavior until June of the following year. The other three males (Fig. 2, B–D) resumed nesting behavior shortly after being released; and their behavior may indicate that they were defending nesting territories before they were captured and tagged. Two of the males ended nesting behavior after one month, and the third appeared to abandon one nesting territory and establish a second when it abruptly started exhibiting nesting behavior at a shallower depth on 14 September 2000 (Fig. 2B). It appears that the male that changed depths may have established a new nest, spawned, and successfully brooded

eggs because nesting behavior ended 89 days later, which is a few days longer than the period needed for eggs to incubate and hatch at the water temperatures recorded by the archival tag (mean=4.9°C). If one considers that this male may have already spent 2 months establishing a nest before being captured and tagged, the total nesting period would be 6.5 months. Given the ambient water temperature and late July start of spawning, there was insufficient time for the other three male Atka mackerel to brood a new or existing batch of eggs. Being displaced from an original nesting territory or failing to attract a female to spawn may be reasons for changing a nesting site or for abandoning it altogether. Nesting colonies can have a broad depth range, cover areas over many square kilometers, and be physically and biologically diverse (Lauth et al., in press); therefore the quality of some territories within a nesting colony may be more suitable for attracting females to spawn.

In addition to males changing the depth and location of their nesting territory, there is evidence to suggest that some male Atka mackerel adopt already existing nesting territories containing eggs. In the exhibit tank at the ASLC, a non-nesting male displaced a territorial nest-guarding male and adopted the egg masses already present on the nest. Adoptive nest behavior is also thought to be a characteristic of another hexagrammid, lingcod (*Ophiodon elongates*) (Withler et al., 2004). Abandoning nests or allowing another fish to assume nest-guarding responsibilities is a common behavior in males that provide parental care of eggs (Gozlan et al., 2003). Male fish that guard territories containing eggs are more reproductively successful because females prefer to mate with males that already have eggs (e.g., Marconato and Bisazza, 1986; DeMartini, 1987; Pruett-Jones, 1992).

There is a high energetic cost to male parental care (Marconato et al., 1993; Gillooly and Baylis, 1999; Steinhart et al., 2005), and protracted nest-guarding severely restricts feeding opportunities for males. Egg cannibalism by males is common in Atka mackerel (Zolotov, 1993; Yang, 1999) and may serve as a means for nest-guarding males to sustain themselves during the protracted nesting season (Zolotov, 1993). Cannibalism of eggs within a male's own nesting territory (filial cannibalism) is considered an adaptive behavior in marine fishes that provide paternal care of eggs and it is especially common in species with protracted breeding cycles (Rowher, 1978; Kondoh and Okuda, 2002).

Commercial trawling on nesting habitat during the spawning and breeding periods would probably result in high mortality of both nest-guarding males and developing embryos. Atka mackerel aggregate for spawning and nesting (Lauth et al., in press), and aggregating behavior is generally predictable and makes a population easier to target and more vulnerable to fishing (Colin et al., 2003). The reproductive success of a fish species is also negatively impacted by alterations to the structural habitat and the benthic

community—alternations that are caused by fishing gears (Auster and Langton, 1999). There is some spatial and temporal overlap of commercial trawling and nesting sites in the Aleutian archipelago (Fritz and Lowe, 1998; Lauth et al., in press), but it is difficult to assess the impacts of the fishery on the reproductive success of Atka mackerel without knowing the total distribution of nesting habitat. Knowledge of the temporal use of breeding habitat can be used as a management tool for minimizing negative impacts of the commercial fishery during crucial periods of Atka mackerel life history.

Conclusions

This study provides detailed information about the timing and duration of three specific phases of the Atka mackerel's reproductive cycle: 1) establishment of a nest, 2) spawning, and 3) egg brooding. An accurate incubation rate from controlled laboratory experiments, egg mass collections from nesting sites, and water temperatures characteristic of those observed at nesting sites were used in an incubation model that showed that nest-guarding males use nesting habitat for more protracted periods than previously known. Model results for the start and end of the reproductive cycle were validated with observations from a time-lapse video camera and archival tags. The duration of the reproductive cycle appears to be affected most by the length of the male brooding phase, which can double in duration within the range of ambient water temperatures observed in our laboratory incubation experiments. Knowledge about the timing and duration of the reproductive cycle is essential for conserving Atka mackerel populations and for providing a solid framework for investigations into the physical and biological processes influencing recruitment and population dynamics.

Acknowledgments

This project was funded by grants from the North Pacific Research Board (# F0417) and the National Marine Fisheries Service (NMFS) Essential Fish Habitat (EFH) fund. Rearing experiments at the Alaska Sealife Center (ASLC) by J. Guthridge were part of the requirements for his Master of Science thesis at the University of Alaska, Fairbanks. R. Lauth thanks the skippers and crew from the FV *Morning Star*, FV *Sea Storm*, FV *Sea-fisher*, and RV *Tiglâx*, especially K. Bell, S. Branstiter, P. Deng, T. Meintz, and S. Clark for field support of this research. Many thanks to S. Atkinson from ASLC for assisting with the proposal and those who helped with field support, scuba diving, or reviewing this manuscript including D. Cooper, G. Duker, G. Hoff, J. Lee, L. Logerwell, S. Lowe, S. McDermott, R. Nelson, K. Rand, C. Rilling, D. Somerton, G. Stauffer, S. VanSant, and two anonymous reviewers.

Literature cited

- Ahlstrom, E. H.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish Wildl. Serv. Spec. Sci. Rep. No. 23:1–26.
- Allen, M. J., and G. B. Smith.
1988. Atlas and zoogeography of common fishes in the Bering Sea and Northeastern Pacific. NOAA Tech. Rep. NMFS 66, 151 p.
- Auster, P. J., and R. W. Langton.
1999. The effects of fishing on fish habitat. In Fish habitat: essential fish habitat and rehabilitation (L. Benaka, ed.), p. 150–187. Am. Fish. Soc., Symposium 22, Bethesda, MD.
- Bailey, K. M.
2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Mar. Ecol. Prog. Ser. 198:215–244.
- Bisazza, A., A. Marconato, and G. Marin.
1989. Male competition and female choice in *Padogobius martensi* (Pisces, Gobiidae). Anim. Behav. 38:406–413.
- Ciannelli, L., K. M. Bailey, K.-S. Chan, A. Belgrano, and N. C. Stenseth.
2005. Climate change causing phase transitions of walleye pollock (*Theragra chalcogramma*) recruitment dynamics. Proc. R. Soc. B 272:1735–1743.
- Colin, P. L., Y. J. Sadovy, and M. L. Domeier.
2003. Manual for the study and conservation of reef fish spawning aggregations, 98 p. Society for the Conservation of Reef Fish Aggregations Special Publication no. 1 (version 1.0), Oceanside, CA.
- Cushing, D. H.
1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26:249–293.
- DeMartini, E. E.
1987. Paternal defense, cannibalism and polygamy: factors influencing the reproductive success of painted greenling (Pisces, Hexagrammidae). Anim. Behav. 35:1145–1158.
- Fritz, L. W., and S. A. Lowe.
1998. Seasonal distributions of Atka mackerel (*Pleurogrammus monopterygius*) in commercially-fished areas of the Aleutian Islands and Gulf of Alaska. U. S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-92, 29 p.
- Gillooly, J. F., and J. R. Baylis.
1999. Reproductive success and the energetic cost of parental care in male smallmouth bass. J. Fish Biol. 54:573–584.
- Gorbunova, N. N.
1962. Spawning and development of greenlings (family Hexagrammidae). In Greenlings: taxonomy, biology, interoceanic transplantation (T. S. Rass, ed.), p. 121–185. Tr. Inst. Okeanol., Akad. Nauk. SSSR 59:118–182. [In Russian.] (translated by Isr. Program. Sci. Trans., 1970). [Available from Natl. Tech. Inf. Serv., Springfield, VA, as TT 69-55097 S.]
- Gozlan, R. E., C. J. Flower, and A. C. Pinder.
2003. Reproductive success in male sunbleak, a recent invasive fish species in the U.K. J. Fish Biol. 63:131–143.
- Haldorson, L., M. Pritchett, D. Sterritt, and J. Watts.
1993. Abundance patterns of marine fish larvae during spring in a southeastern Alaskan bay. Fish. Bull. 91:36–44.
- Hempel, G.
1979. Early life history of marine fish: the egg stage, 70 p. Washington Sea Grant, Seattle, WA.
- Hutchings, J. A., and R. A. Myers.
1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser., 108:21–31
- Kendall, A. W., and J. R. Dunn.
1985. Ichthyoplankton of the continental shelf near Kodiak Island, Alaska. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-20, 89 p.
- Kenyon, K. W.
1965. Food of harbor seals at Amchitka. J. Mamm. 46:103–104.
- Kondoh, M., and N. Okuda.
2002. Mate availability influences filial cannibalism in fish with paternal care. Anim. Behav. 63:227–233.
- Ladd, C., G. L. Hunt, Jr., C. W. Mordy, S. Salo, and P. Stabeno.
2005. Marine environment of the eastern and central Aleutian Islands. Fish. Oceanogr., 14(Suppl. 1): 22–38.
- Lauth, R. R., S. W. McEntire, and H. H. Zenger.
In press. Geographic distribution, depth range, and description of Atka mackerel (*Pleurogrammus monopterygius*) nesting habitat in Alaska. Alaska Fish. Res. Bull.
- Lauth, R. R., and D. M. Blood.
2007. Description of embryonic development of Atka mackerel (*Pleurogrammus monopterygius*). Fish. Bull. 105:571–576.
- Lowe, S., J. Ianelli, M. Wilkins, K. Aydin, R. Lauth, and I. Spies.
2006. Stock assessment of Aleutian Islands Atka mackerel. In Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 949–1016. North Pacific Fishery Management Council, Anchorage, AK.
- Marconato, A., and A. Bisazza.
1986. Males whose nests contain eggs are preferred by female *Cottus gobio* L. (Pisces: Cottidae). Anim. Behav. 34:1580–1582.
- Marconato, A., A. Bisazza, and M. Fabris.
1993. The cost of parental care and egg cannibalism in the river bullhead, *Cottus gobio* L. (Pisces: Cottidae). Behav. Ecol. Sociobiol. 32:229–237.
- McDermott, S. F., and S. A. Lowe.
1997. The reproductive cycle of Atka mackerel, *Pleurogrammus monopterygius*, in Alaska waters. Fish. Bull. 95:321–333.
- McDermott, S. F., K. Pearson, and D. Gunderson.
2007. Annual fecundity, batch fecundity, and oocyte atresia of Atka mackerel (*Pleurogrammus monopterygius*) in Alaska waters. Fish. Bull. 105:19–29.
- Medveditsyna, A. V.
1962. Data on the Atka mackerel (*Pleurogrammus monopterygius* (Pallas)). In Greenlings: taxonomy, biology, interoceanic transplantation (T. S. Rass, ed.), p.104–106. Tr. Inst. Okeanol., Akad. Nauk. SSSR 59:101–103. In Russian (translated by Isr. Program. Sci. Trans., 1970). [Available from Natl. Tech. Inf. Serv., Springfield, VA, as TT 69-55097 S.]
- Murie, O. J.
1959. Fauna of the Aleutian Islands and Alaska Pen-

- insula. U.S. Fish Wildl. Serv., North American Fauna 61:395–406
- Napp, J. M., A. W. Kendall Jr., and J. D. Schumacher.
2000. A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. *Fish. Oceanogr.* 9:147–162
- Nichol, D. G., and D. A. Somerton.
2002. Diurnal vertical migration of the Atka mackerel *Pleurogrammus monopterygius* as shown by archival tags. *Mar. Ecol. Prog. Ser.* 239:193–207.
- Ohshima, K. I., Y. Fukamachi, T. Mutoh, and M. Wakatsuchi.
2005. A generation mechanism for mesoscale eddies in the Kuril Basin of the Okhotsk Sea: baroclinic instability caused by enhanced tidal mixing. *J. Oceanogr.* 61:247–260.
- Ojaveer, E., and M. Kalejs.
2005. The impact of climate change on the adaptation of marine fish in the Baltic Sea. *ICES J. Mar. Sci.* 62:1492–1500.
- Östlund-Nilsson, S.
2000. Are nest characters of importance when choosing a male in the fifteen-spined stickleback (*Spinachia spinachia*)? *Behav. Ecol. Sociobiol.* 48(3):229–235.
- Pruett-Jones, S.
1992. Independent versus nonindependent mate choice: do females copy each other? *Am. Nat.* 140:1000–1009.
- Riley, J. D.
1974. The distribution and mortality of sole eggs (*Solea solea* L.) in inshore areas. In *The early life history of fish* (J. H. S. Blaxter, ed.) p. 39–52. Springer, Heidelberg, Germany.
- Rodionov, S. N., J. E. Overland, and N. A. Bond.
2005. Spatial and temporal variability of the Aleutian climate. *Fish. Oceanogr.* 14 (suppl.) 1:3–21.
- Rohwer, S.
1978. Parent cannibalism of offspring and egg raiding as a courtship strategy. *Am. Nat.* 112:429–440.
- Ruttenberg, E. P.
1962. Survey of the fishes family Hexagrammidae. In *Greenlings: taxonomy, biology, interoceanic transplantation* (T. S. Rass, ed.), p.1–103. *Tr. Inst. Okeanol., Akad. Nauk. SSSR* 59:3-100. In Russian (translated by Isr. Program. Sci. Trans., 1970). [Available from Natl. Tech. Inf. Serv., Springfield,VA, as TT 69-55097 S.]
- Sargent, R. C.
1982. Territory quality, male quality, courtship intrusion and female nest-choice in the three-spined stickleback, *Gasterosteus aculeatus*. *Anim. Behav.* 30:364–374.
- Sikkel, P. C.
1988. Factors influencing spawning site choice by female garibaldi, *Hypsypops rubicundus* (Pisces: Pomacentridae). *Copeia* 1988:710–718.
- Sinclair E. H., and T. K. Zeppelin.
2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *J. Mamm.* 83:973–990.
- Steinhart, G. B., M. E. Sandreneb, S. Weavera, R. A. Steina, and E. A. Marschalla.
2005. Increased parental care cost for nest-guarding fish in a lake with hyperabundant nest predators. *Behav. Ecol.* 2005 16(2):427–434.
- Wieland, K., A. Jarre-Teichmann, and K. Horbowa.
2000. Changes in the timing of spawning Baltic cod: possible causes and implications for recruitment. *ICES J. Mar. Sci.* 57:452–464.
- Withler R. E., J. R. King, and J. B. Marliave.
2004. Polygamous mating and high levels of genetic variation in lingcod (*Ophiodon elongatus*) of the Strait of Georgia, British Columbia. *Environ. Biol. Fishes* (69):345–357.
- Yang, M-S.
1999. The trophic role of Atka mackerel, *Pleurogrammus monopterygius*, in the Aleutian Islands area. *Fish. Bull.* 97(4):1047–1057.
- Zar, J. H.
1999. *Biostatistical analysis*, 4th ed., 663 p. Prentice-Hall, Inc., Englewood Cliffs, NJ.
- Zenger, H. H., Jr.
2004. Data report: 2002 Aleutian Islands bottom trawl survey. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-143, 247 p.
- Zolotov, O. G.
1993. Notes on the reproductive biology of *Pleurogrammus monopterygius* in Kamchatka waters. *J. Ichthyol.* 4:25–37.